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BULLETIN

OF THE

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THE TORREY BOTANICAL CLUB

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JULY, 1916

Phytogeographical notes on the Rocky Mountain region VI. Distribution of the subalpine plants

P. A. RYDBERG

I have already pointed out in a paper entitled "Vegetative Life Zones of the Rocky Mountains," read at the twentieth anniversary of the New York Botanical Garden, that the Subalpine and Montane Zones of the Rockies are very different from those zones in the eastern part of North America, although the Hudsonian and Canadian Zones extend west to the foot of the Rockies from the headwaters of the Athabasca River northward. Also, I showed that the aspen was the only one among the ecologically important trees, common to the eastern and central (Rocky Mountain) provinces, that the Subalpine and Montane Zones of the central and western (Pacific) provinces merge in the north, and that many species have emigrated from either of these provinces to the other. These statements were largely based on the most conspicuous element of these zones, namely, the forest trees. Now it is to be shown whether or not these statements apply to the secondary species of the forests, to the grasslands and other herbaceous formations, and to the coppice.

The subalpine flora may be divided into the following categories:—I. The transcontinental element, many members of which are also found in the Old World; II. Plants common to the Rockies and either of the other provinces; III. The endemic element. To the first belong the larger proportion of the plants common to the alpine-arctic zone.

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Some of the plants of the first category may have a range limited in the Middle Province to the Canadian Rockies alone; others may extend throughout the Northern Rockies, but not be found in the Southern; while still others may extend throughout the Rocky Mountain system. Of the second category, some plants may be common to the Rockies and the Hudsonian Zone of the east, some others common to the Rockies and the Pacific mountains, or to the Sierra Madre in Mexico, or to the Alaskan mountains, or to the arctic coast. Some might have their home in the Rockies and spread to other regions, and others might be immigrants into the Rocky Mountain system. Among the plants of the third category, many are distributed throughout the Rockies, others have a distribution limited to either the Northern or the Southern Rockies, or to certain parts of either, while still others are purely local.

The strictly subalpine element of the flora of the Rockies is in fact very small, the plants consisting mostly of species that are found also in the Montane Zone, especially the upper part thereof, and of alpine-arctic species, running down in the swales, along the streams, or along the wind-swept hog-backs. In fact some plants, especially aquatics and hydrophytes, are common to three or more zones. In the following lists the plants common to the alpine-arctic zone are designated by a dagger (†). No attempt is made to designate those common to the Montane Zone, as they would probably constitute 90 per cent. of the remaining species.

I

1. TRANSCONTINENTAL SPECIES RANGING THROUGHOUT THE ROCKIES

This element is represented among the trees by the quaking aspen, *Populus tremuloides*,* but this tree is not one of the characteristic trees of the Subalpine or Subarctic Zone either of the east or of the Rockies, nor is it limited to the subalpine regions. One should therefore not lay too much stress upon this tree and its

* It is true that some botanists, such as Tidestrom, Wooton and Standley, regard the Rocky Mountain aspen as a distinct species, *Populus aurea*, differing in smaller, thicker, less toothed leaves and different colored anthers and bark, but as the distribution of this species has not been worked out, it is better here to ignore the same and include it in *P. tremuloides*.

distribution when considering the resemblances of and distinctions between the Hudsonian flora and the subalpine flora of the Rockies. Looking over the following two lists we find that they are mostly made up of either aquatic plants and hydrophytes or plants from dense or open woods or copses, requiring a good deal of moisture.

Trees

Populus tremuloides

Shrubs

Salix chlorophylla
Betula glandulosa
Lepargyrea canadensis
Vaccinium caespitosum
Linnaea americana
Distegia involucrata

Herbs

Sparganium minimum
" *angustifolium*
Potamogeton natans
" *alpinus*
" *heterophyllus*
" *Richardsonii*
" *pectinatus*
" *filiformis*
Triglochin palustris
" *maritima*
Scheuchzeria palustris
Savastana odorata
Muhlenbergia racemosa
Phleum pratense
" *alpinum*
Alopecurus aristulatus
" *occidentalis*
Agrostis hiemalis
" *canina*
Calamagrostis Langsdorfii
" *canadensis*
" *purpurascens*
Deschampsia caespitosa
" *atropurpurea*
Avena striata
Danthonia intermedia
Trisetum subspicatum
Phragmites Phragmites
†*Catabrosa aquatica*
Bromus ciliatus
Poa pratensis
† " *alpina*
" *crocata*
†*Festuca curtifolia*
Panicularia nervata
Hordeum jubatum
Agropyron violaceum
Eriophorum angustifolium
†*Carex Hepburnii*
" *leptalea*
† " *obtusata*
† " *gynocrates*
" *siccata*
" *interior*
" *canescens*
" *brunnescens*
" *Rossii*
" *aurea*

†*Carex capillaris*
" *misandra*
" *Halleri*
† " *atrata*
" *rostrata*
Lemna minor
†*Juncus triglumis*
† " *castaneus*
Juncoides parviflorum
† " *spicatum*
" *intermedium*
†*Lloydia serotina*
Vagnera stellata
Lysiella obtusata
Peramium ophioides
†*Cytherea bulbosa*
†*Oxyria digyna*
†*Bistorta vivipara*
Alsine longifolia
" *laeta*
" *crassifolia*
" *borealis*
Moehringia macrophylla
" *lateriflora*
Sagina saginoides
†*Silene acaulis*
Anemone parviflora
Pulsatilla ludoviciana
†*Thalictrum alpinum*
Batrachium confervoides
†*Draba crassifolia*
† " *fladnizensis*
† " *aurea*
†*Chrysosplenium tetrandrum*
†*Saxifraga cernua*
Leptasea Hirculus
†*Sibbaldia procumbens*
†*Potentilla quinquefolia*
† " *nivea*
† " *uniflora*
Dasiphora fruticosa
Geum rivale
Tium alpinum
Epilobium alpinum
" *Hornemannii*
† " *anagallidifolium*
Chamaenerion angustifolium
† " *latifolium*
Hippurus vulgaris
Moneses uniflora
Pyrola uliginosa
" *chlorantha*
" *minor*
" *secunda*
Menyanthes trifoliata
Veronica americana
" *Wormskioldii*
" *serpyllifolia*
†*Elephantella groenlandica*
Utricularia vulgaris
" *minor*
Campanula petiolata
Erigeron jucundus
" *compositus*
Artemisia spithamaea

2. TRANSCONTINENTAL SPECIES CONFINED TO THE NORTHERN ROCKIES

The number of transcontinental plants found in the Northern Rockies, but not in the Southern, is much smaller, and of these a

larger percentage are arctic-alpine, descending into the Subalpine Zone. Among these plants there are no trees and only a few low shrubs.

Shrubs

†*Salix pseudomyrsinites*
Ribes hudsonianum
Andromeda polifolia
Chiogenes hispidula
Vaccinium uliginosum

Herbs

†*Eriophorum Chamissonis*
†*Scirpus pauciflorus*
† " *caespitosus*
†*Carex capitata*
" *aenea*
" *Heleonastes*
† " *supina*
" *deflexa*
" *Hassei*
" *livida*
" *vaginata*
" *atratiformis*
" *miliaris*
" *scirpoidea*
†*Juncoides hyperboreum*
Cypripedium passerinum
†*Ranunculus hyperboreus*
Drosera rotundifolia
Parnassia palustris
† " *Kotzebuei*
†*Saxifraga rivularis*
Anthiphylla oppositifolia
Comarum palustre
Mertensia paniculata
Veronica scutellata
†*Pinguicula vulgaris*
Valeriana septentrionalis
Erigeron alpinus
" *unalaschkensis*
" *purpureum*
Senecio pauciflorus

3. TRANSCONTINENTAL SPECIES LIMITED TO THE CANADIAN ROCKIES

Some of the transcontinental subarctic plants have not spread at all south in the mountains and are found in the Rockies only at an altitude where the Subarctic Zone covers the lowlands. In other words, they are found only in the Canadian Rockies. These plants are also found north of the arctic timberline. They are:

Shrubs

†*Rubus acaulis*
† " *Chamaemorus*
†*Ledum groenlandicum*
†*Cassiope tetragona*
†*Vaccinum Vitis-Idaea*
†*Oxycoccus Oxycoccus*

Herbs

†*Eriophorum Scheucheri*
† " *alpinum*
†*Juncoides arcticum*
† " *arcuatum*
†*Orchis rotundifolia*
†*Arenaria norvegica*
†*Drosera longifolia*
†*Condrosea Aizoon*
†*Leptasea tricuspidata*

II

1. Species nearly equally distributed in the Rockies and the Pacific mountains

There are many species which seem equally at home both in the Rocky Mountains, the Sierra Nevada and the Cascade Mountains. The larger part of these are more or less xerophytic plants growing in the drier part of the subarctic zone, especially on southern exposures. Nearly all of the plants listed below are also equally distributed in the Montane and the Subalpine Zones. To these belong four of the conifers, *Pseudotsuga mucronata*, *Pinus Murrayana*, *P. flexilis* and *P. albicaulis*. Of these the last mentioned is the only one which is not better represented in the Montane Zone. Its distribution is also more extensive in the Pacific mountains, and it is not found in the Southern Rockies. It has therefore been placed among the immigrants, though its original home might be the Northern Rockies. *Pseudotsuga mucronata* is also found in the mountains of northern Mexico. All extend north in the Rockies to about latitude 55 degrees, except *Pinus Murrayana*, which grows much further north in the Yukon Valley, at latitude 65 degrees.

Trees

Pseudotsuga mucronata
Pinus Murrayana
Pinus flexilis

Shrubs

Salix glaucops
Ribes montigenum
Pachystima myrsinites
Phyllodoce empetriformis
Ledum glandulosum
Kalmia microphylla
Gaultheria humifusa

Herbs

Muhlenbergia comata
Agrostis asperifolia
" *variabilis*
Danthonia californica
Graphephorum muticum
Poa longiligula
" *Fendleriana*
Bromus polyanthus
Panicularia pauciflora
Elymus glaucus
†*Carex nigricans*
" *Douglasii*
" *illota*
" *athrostachya*
" *phaeocephala*
" *festivella*
" *Reynoldsii*
" *nova*
Lemna gibba
Veratrum speciosum
†*Juncus Drummondii*
† " *Parryi*
" *Mertensianus*
Eriogonum umbellatum
†*Bistorta bistortoides*
Alsine bailcalensis
" *calycantha*
†*Cerastium beeringianum*
Alsinopsis Nuttallii
Nymphaea polysepala
Anemone globosa
Ranunculus Eschscholtzii
Aconitum columbianum
Cardamine umbellata
*Draba nitida**
† " *oligosperma*
†*Rhodiola integrifolia*
Parnassia fimbriata
Pectianthia pentandra
Micranthes arguta
Ivesia Gordonii
Potentilla diversifolia
Fragaria bracteata
Gayophytum racemosum
Amarella strictiflora
" *plebeia*
Leptodactylon Nuttallii
Phacelia heterophylla
Pentstemon procerus
Mimulus Langsdorfii
Pedicularis racemosa
" *bracteata*
Erigeron simplex
" *Coulteri*
" *salsuginosus*
†*Antennaria media*
" *rosea*
Dugaldia Hoopesii‡
Achillea lanulosa
Arnica pedunculata
" *cordifolia*

2. SPECIES COMMON TO THE ROCKIES AND THE MOUNTAINS OF THE GREAT BASIN

A few plants are distributed through a larger or smaller part of the Southern Rockies (especially the Wasatch Mountains of Utah

* Lacking in Colorado.

‡ In the Southern Rockies only.

and the Bear River Mountains of Idaho) and of the higher mountains of the Great Basin extending to the eastern slopes of the Sierra Nevada. These plants are very few in the Subalpine Zone, more in the Montane, and still more in the Submontane and Upper Sonoran. Some of these are listed under the endemic element of the Rockies, as it is very hard to tell whether their original homes are in the Rockies or in the Basin mountains. To this element belongs one tree, *Pinus aristata*, growing on dry southern slopes from Colorado west to eastern California. It is perhaps more frequently met with in Colorado, but it might have originated on the eastern slopes of the Sierra Nevada, as its only close relative, *P. Balfouriana*, is also found there. The following is a partial list of the plants of this category:

Tree

Pinus aristata

Herbs

†*Erigeron Kingii*
†*Draba pectinata*
Ivesia utahensis
Drymocallis pumila
Kentrophyta tegetaria
Macronema discoidea
Senecio seridophyllus

3. SPECIES COMMON TO THE NORTHERN ROCKIES AND THE CASCADE MOUNTAINS

As the Northern Rockies and the Cascades are connected by several mountain chains in British Columbia, it is very hard to decide where these common plants should be counted, to the Rocky Mountain flora or to the flora of the Cascades. It is probable that to the former should be counted those which are generally distributed in the main chain of the Rockies in Alberta and Montana, especially if their range extends south into the Yellowstone Park. I would even include in the Rocky Mountain flora such species as *Larix Lyallii* (although very local), which crosses the main range at a few places, while I would count *Tsuga Mertensiana*, which extends east only to the Bitter Root and Selkirk Mountains, to the Cascade element.

a. ROCKY MOUNTAIN ELEMENT

Tree

Larix Lyallii

Shrubs

Ribes petiolaris
†*Phyllodoce glanduliflora*

Herbs

Carex Tolmiei
Tofieldia intermedia
Erythronium grandiflorum
Eriogonum Piperi
" *polyphyllum*
†*Draba lonchocarpa*
Ozomelis trifida
Heuchera ovalifolia
Drymocallis pseudorupestris
Atragallus spicatus
Hedysarum sulphurescens
Amarella anisopetala
Pentstemon crassifolium
Castilleja lutea
" *pallescens*
Erigeron pedatus
Antennaria corymbosa
†*Senecio Fremontii*

b. CASCADE ELEMENT

Tree

Tsuga Mertensiana

Shrubs

Salix Barclayi
" *subcaerulea*
Alnus sinuata
Rubus nivalis
Azaliastrum albiflorum
Gaultheria ovatifolia

Herbs

Carex laeviculmis
" *stenochlaena*
" *Mertensii*
Juncoides glabratum
Alnus sinuata
Silene oregana
†*Ranunculus Suksdorfii*
Aquilegia columbiana
†*Smelowskia ovalis*
Arabis Lyallii
Hemieva ranunculifolia
†*Lutkea pectinata*
Viola adunca
Osmorrhiza Leibergii
Pentstemon fruticosus
Synthyris reniformis

Most of these extend to the western slopes of the Rockies in British Columbia or northern Montana, but *Tsuga Mertensiana*, *Osmorrhiza Leibergii* and *Synthyris reniformis* are restricted to the western slopes of the Bitter Root Mountains in Idaho.

4. Western immigrants from the Sierra Nevada and the Cascades, which have invaded the Northern Rockies

There are a number of species which are common to the Pacific mountains and the Rockies, but have a wider distribution in the former than in the latter. Their home may therefore be regarded as being on the west coast, and they may be regarded as immigrants into the Rocky Mountains. Those of the following list are common to the Sierra Nevada and the Cascades, and their range extends into the Northern Rockies. Some of these are found in the Bitter Root or the Selkirk Mountains only, and are without doubt immigrants. Others extend into the main Rockies of Alberta and Montana and even as far south as northern Wyoming. Whether these are immigrants or endemics to the Rockies is more doubtful. A very few reach the Wasatch Mountains in northern Utah. There are no immigrants from the Sierras to the southern Rockies. It is true that there are a few subalpine endemics common to the Sierra Nevada and the Southern Rockies, but these are plants characteristic of the mountains of the Great Basin, and limited to the eastern slope of the Sierra Nevada and the western slope of the Rockies.

Trees

Pinus albicaulis
Salix sitchensis

Shrubs

†*Salix cascadensis*
Ribes laxiflorum
Ribes glandulosum
Cassiope Mertensiana
Vaccinium occidentale
Linnaea longiflora

Herbs

Stipa oregonensis
Poa Cusickii
Carex spectabilis
Xerophyllum tenax

Juncus Regelii
" *nevadensis*
Cytherea occidentalis
†*Eriogonum pyrolaefolium*
Naiocrene parvifolia
†*Arenaria salmonensis*
Anemone Drummondii
Pulsatilla occidentalis
Ranunculus alismellus
Aquilegia formosa
Thlaspi californicum
Dentaria rupicola
Draba eurocarpa
Pectianthia Breweri
Heuchera glabra
Potentilla flabellifolia
Epilobium oregonense
" *luteum*
†*Dasystephana calycosa*
Romanzoffia sitchensis
Adenostegia ramosa
†*Pedicularis contorta*

Of these *Eriogonum pyrolaefolium*, *Draba eurocarpa*, *Potentilla flabellifolia* and *Linnaea longiflora* are limited to the Bitter Root-Selkirk region, while *Pinus albicaulis* and *Stipa oregonensis* extend south to Wyoming, and *Vaccinium occidentale* to northern Utah.

5. IMMIGRANTS FROM ALASKA AND THE ARCTIC COAST

The following are mostly arctic, a few being subarctic plants from near the arctic timber line, which extend farther south in the Rockies and are there found in the subalpine as well as the alpine zone. Of these *Silene repens*, *Micranthes Lyallii*, *Dasystephana glauca* and *Euphrasia mollis* extend as far south as Montana; the others are limited to the Canadian Rockies.

Shrubs

†*Salix myrtillifolia*
† " *alaxensis*
† " *Barrattiana*
† " *Seemanii*
" *Drummondiana*
Salix arbusculoides
" *desertorum*
" *saskatchewana*
†*Arctous erythrocarpa*

Herbs

Carex venustula
" *physocarpa*
" *MacCallae*
Silene repens
†*Anemone Richardsonii*
Aconitum delphinifolium
Sophia sophioides
Pilosella Richardsoniana
Arabis ambigua
Micranthes Lyallii

Micranthes aestivalis
Spathularia Brunnoniana
" *ferruginea*
Argentina subarctica
†*Hedysarum Mackenzii*
Moneses reticulata
*Androsace septentrionalis**
†*Amarella propinqua*
†*Dasystephana glauca*
†*Castilleja pallida*
Euphrasia mollis
Valeriana sitchensis
†*Campanula heterodoxa*
Erigeron grandiflorum
Erigeron lanatus
†*Antennaria monocephala*
†*Artemisia Richardsoniana*
Petasites frigida
" *corymbosa*
Senecio lugens

6. IMMIGRANTS FROM THE SOUTH

Immigrants from the south are almost unknown in the Subalpine Zone; they are more frequent in the Montane and Submontane Zone and are very common in the Sonoran. The following are the only ones found in the subalpine zone:

Pseudocymopterus purpureus *Blepharineuron tricholepis*

III

1. ENDEMIC SPECIES, WHICH ALSO HAVE EMIGRATED INTO THE CASCADE MOUNTAINS

The endemic element of the Rocky Mountains is by far the largest. As the Rockies and the Cascades are connected through several mountain chains it is natural that many of the endemic Rocky Mountain species should have emigrated into the Cascade Mountains. Let us treat these species first.

The dominant tree in the Subalpine Zone is, as already stated in a previous article,† the Engelmann spruce, *Picea Engelmannii*. Often associated with it is found the subalpine fir, *Abies lasiocarpa*. Both extend throughout the Rockies from about latitude 55 degrees southward to the higher mountains of New Mexico and Arizona. They are also found in the northern portion of the western or Pacific province, i.e. throughout the Cascades, but not in the Sierra Nevada region. They are not found in the eastern province but are represented there by *Picea canadensis*, *P. mariana*, and *Abies balsamea*. Although the two species of *Picea* have been reported

* Also in Europe.
† See Bull. Torrey Club 42: 11. Ja 1915.

from Alberta and Montana, all specimens referred to these and seen by me have turned out to belong to *Picea albertiana*. *Picea Engelmannii* and *Abies lasiocarpa* may be regarded as endemic Rocky Mountain species, which have emigrated into the Cascades. In the Northern Rockies there could be added to these *Larix Lyallii*, which has also emigrated into the northern part of the Cascades. In the very lowest part of the Subalpine Zone there are sometimes found intermixed trees of *Pseudotsuga mucronata* belonging really to the Montane Zone. It has about the same distribution in the Rockies as the spruce and fir mentioned above, but is also equally common though in the Pacific province and extends south into the Sierra Madre of Mexico. It is hard to tell if its original home was in the Rockies or on the Pacific coast.

The two species, *Picea Engelmannii* and *Abies lasiocarpa*, are not restricted to the Subalpine Zone, however, for both run down into the Montane Zone on northern slopes and along streams. The element of the Rocky Mountain flora, which has the same distribution as these, is, as stated before, not large and it contains no other woody plants.

Trees

Picea Engelmannii	*Abies lasiocarpa*

Herbs

Trisetum majus	*Arabis rupestris*
Poa reflexa	" *Drummondii*
" *leptocoma*	*Lithophragma bulbifera*
" *Paddensis*	*Ozomelis stauropetala*
" *nevadensis*	*Leptasea austromontana*
† " *rupicola*	†*Sieversia ciliata*
†*Festuca saximontana*	*Epilobium Drummondii*
Carex Engelmannii	†*Phlox caespitosa*
" *pyrenaica**	*Macronema grindelifolium*
" *petasata*	*Aster apricus*
" *Geyeri*	*Anaphalis subalpina*
Juncus balticus montanus	*Antennaria umbrinella*
Ophrys nephrophylla	" *anaphaloides*
Trollius albiflorus	*Arnica Parryi*
Cardamine acuminata	" *Rydbergii*

* Also in Europe and Asia.

2. ENDEMIC SPECIES, COMMON TO THE NORTHERN AND SOUTHERN ROCKIES

The endemic element, which extends over the whole Rockies, but has not invaded the Cascades, is much larger, but it does not include any of the forest trees and only a few shrubs. It consists of the following species:

Shrubs

†*Salix petrophila*
† " *saximontana*
" *brachycarpa*
Ribes parvulum
†*Vaccinium oreophilum*
" *scoparium*

Herbs

Potamogeton interior
Stipa Tweedyi
" *minor*
" *Nelsonii*
Deschampsia curtifolia
Poa Olneyi
" *Buckleyana*
" *epilis*
" *laevigata*
Bromus Porteri
" *Pumpellianus*
Festuca ingrata
Agropyrum andinum
" *Scribneri*
Carex pseudoscirpoidea
† " *albonigra*
† " *chalciolepis*
† " *scopulorum*
† " *chimaphila*
Allium brevistylum
*Disporum trachycarpum**
Ophrys borealis
Eriogonum flavum
Bistorta linearifolia
†*Claytonia megarrhiza*
†*Oreobroma pygmaea*
Alsine strictiflora‡
Cerastium scopulorum
" *strictum*
†*Alsinopsis propinqua*
† " *obtusiloba*
Silene Douglasii
" *Menziesii*
†*Anemone zephyra*
Thalictrum venulosum
Atragene tenuiloba
†*Ranunculus affinis*
† " *eximius*
" *alpeophilus*
Aquilegia caerulea
Thlaspi glaucum
†*Smelowskia americana*
Radicula alpina
†*Draba andina*
" *crassa*
†*Clementsia rhodantha*
Heuchera parviflora
†*Saxifraga debilis*

* East to Manitoba and the Black Hills.
‡ East to Quebec.

†*Muscaria adscendens**
" *delicatula*
†*Micranthes rhomboidea*
" *arnoglossa*
†*Spathularia Vreelandii*
Potentilla filipes
" *glaucophylla*
" *divisa*
† " *saximontana*
" *arachnoidea*
Fragaria glauca
†*Acomastylis turbinata*
Lupinus parviflorus
" *caespitosus*
†*Trifolium nanum*
Atelephragma elegans
Aragallus deflexus
†*Epilobium clavatum*
" *wyomingense*
Osmorrhiza obtusa
†*Vaccinium oreophilum*
" *scoparium*
†*Primula Parryi*
†*Androsace carinata*
" *subumbellata*
" *filiformis*
Anthropogon elegans
†*Dasystephana Romanzovii*
† " *affinis*
Pleurogyne fontana
Swertia scopulina
† " *congesta*
Leptodactylon pungens
†*Phlox depressa*
Phlox Kelseyi
" *alyssoides*
†*Phacelia sericea*
† " *ciliosa*
†*Eritrichum elongatum*
*Myosotis alpestris**
Besseya gymnocarpa
Castilleja rhexifolia
" *lanata*
" *lancifolia*
† " *occidentalis*
Valeriana edulis
Solidago scopulorum
† " *ciliosa*
" *oreophila*
Chrysopsis pumila
†*Aster alpinus**
" *Fremontii*
†*Erigeron trifidus*
" *glabellus*
" *flagellaris*
Antennaria microphylla
" *sedoides*
" *aprica*
Chaenactis alpina
†*Rydbergia grandiflora*
Achillea subalpina
†*Artemisia scopulorum*
Arnica subplumosa
" *rhizomata*
" *pumila*
†*Senecio Purshianus*
" *cymbalarioides*
" *pseudaureus*

3. ENDEMIC SPECIES LIMITED TO THE NORTHERN ROCKIES

The following endemics are not merely local but are practically limited to the Northern Rockies:

* Also in Europe.

Shrubs

†*Salix Tweedyi*
Salix Fernaldii

Herbs

*Alopecurus caespitosus**
Agrostis idahoensis
Poa nervosa
" *confusa*
Sitanion rigidum
Agropyron latiglume
Xerophyllum Douglasii
Erythronium obtusum
Eriogonum caespitosum
" *heracleoides*
Spraguea multiceps
†*Alsine americana*
Arenaria lithophila
†*Silene Lyallii*
" *multicaulis*
Anemone tetonensis
" *lithophila*
Ranunculus saxicola
" *Helleri*
†*Caltha leptosepala*
†*Aquilegia Jonesii*
†*Smelowskia lobata*
†*Draba densiflora*
Arabis oreophila
" *exilis*
Coniomitella Williamsii
Heuchera flabellifolia
" *grossularifolia*
†*Telesonix heucheriformis*
†*Muscaria monticola*
†*Micranthes Rydbergii*
" *occidentalis*
† " *saximontana*
Potentilla glomerata
" *perdissecta*
" *Macounii*
" *ovina*
†*Acomastylis sericea*
Lupinus pulcherrimus
" *monticola*
Trifolium Haydeni
† " *montanense*
Cystium platytropus‡
Atelophagma Forwoodii
" *debilis*
Homalobus Bourgovii
†*Aragallus foliolosus*
† " *alpicola*
† " *viscidus*
† " *viscidulus*
Viola flavovirens
Epilobium latiusculum
" *saximontanum*
Ligusticum filicinum
Pseudoreoxys bipinnata
Angelica Roseana
Bupleurum americanum
" *purpureum*
Vaccinium globularis
†*Douglasia montana*
†*Dasystephana monticola*
Polemonium pulcherrimum
† " *viscosum*
†*Collomia debilis*
†*Phlox costata*
† " *diapensioides*

* Canadian Rockies only.
‡ Also in Nevada.

Phacelia alpina
† " *Lyallii*
Mertensia stenoloba
† " *Tweedyi*
Pentstemon Lyallii
† " *montanus*
" *aridus*
" *pseudohumilus*
" *Tweedyi*
Synthyris laciniata
" *dissecta*
†*Castilleja Tweedyi*
† " *pulchella*
†*Pedicularis ctenophora*
† " *cystopteridifolia*
Oreostemma Haydeni
†*Erigeron radicatus*
Hulsea carnosa
Senecio sphaerocephalus
† " *alpicola*
" *megacephalus*

Some of these endemics of the Northern Rockies extend south into the Wasatch Mountains of Utah. As I have already stated, the exchange of species between the Northern and Southern Rockies does not take place along the continental divide in Wyoming, but between the Wasatch and Teton Mountains, through the Bear River Mountains in southeastern Idaho. This exchange is more evident in the Montane Zone, but the following northern endemics have crossed the line and their range extends into Utah:

Eriogonum heracleoides
Arabis oreophila
Anemone tetonensis
Potentilla Macounii
Ligusticum filicinum
Angelica Roseana
Vaccinium globulare
Polemonium viscosum
Collomia debilis
Synthyris laciniata

A few of the northern endemics extend eastwards into the Black Hills of South Dakota such as:

Atelephragma Forwoodii
Epilobium saximontanum

4. ENDEMIC SPECIES RESTRICTED TO THE SOUTHERN ROCKIES

The endemics are more numerous in the Southern Rockies than in the Northern. The more widely distributed are the following:

Shrubs

Salix pseudolapponum
" *Wolfii*
Ribes coloradensis
Ribes Wolfii
Sambucus microbotrys

Herbs

Muhlenbergia Wolfii
" *subalpina*
" *filiculmis*
" *gracilis*
†*Deschampsia alpicola*
†*Avena Mortoniana*
Trisetum montanum
Graphephorum Wolfii
†*Poa alpicola*
" *Vaseyana*
" *occidentalis*
" *lucida*
" *aperta*
" *longipedunculata*
" *Sheldoni*
† " *Pattersoni*
" *Traceyi*
† " *Grayana*
† " *Lettermanii*
Festuca arizonica
" *Thurberi*
† " *minutiflora*
Elymus simplex
Carex elynoides
" *occidentalis*
" *Egglestonii*
" *eburnea*
" *Nelsonii*
† " *bella*
Veratrum tenuipetalum
Anticlea coloradensis
Juncus Hallii
" *parous*
Juncoides subapetalum
Erythronium parviflorum
Sisyrinchium alpestre
Limnorchis purpurascens
Eriogonum arcuatum
" *chloranthum*
" *neglectum*
†*Paronychia pulvinata*
Cerastium Earlei
" *variabile*
" *oreophilum*
Alsinopsis macrantha
Arenaria confusa
" *Tweedyi*
" *Fendleri*
Silene Hallii
†*Wahlbergella montana*
*Ranunculus alismaefolius**
" *Macauleyi*
" *micropetalus*
† " *adoneus*
† " *stenolobus*
†*Caltha rotundifolia*
†*Aquilegia saximontana*
" *elegantula*
" *oreophila*
Aconitum Bakeri
" *insigne*
Delphinium occidentale
" *Barbeyi*
†*Thlaspi coloradense*
† " *purpurascens*
†*Smelowskia lineariloba*
Lesquerella parvula
" *montana*
Sophia purpurascens
Cheirinia oblanceolata
" *nivalis*
† " *radicata*
† " *amoena*
†*Draba Parryi*

* North to Wyoming.

Draba chrysantha
" *graminea*
" *streptocarpa*
" *spectabilis*
" *luteola*
" *aureformis*
†*Rhodiola polygama*
Ozomelis stenopetala
" *Parryi*
Heuchera flavescens
†*Telesonix Jamesii*
†*Saxifraga simulata*
†*Micranthes brachypus*
†*Leptasea chrysantha*
Potentilla modesta
" *viridior*
" *decurrens*
Drymocallis fissa
†*Trifolium stenolobum*
† " *lividum*
† " *dasyphyllum*
" *Brandegei*
† " *Parryi*
Homalobus humilis
Aragallus oreophilus
" *Parryi*
Lathyrus arizonicus
Geranium Pattersonii
Viola neomexicana
" *bellidifolia*
Epilobium ovatifolium
" *stramineum*
Ligusticum Porteri
Ligusticella Eastwoodiae
†*Oreoxis humilis*
† " *Bakeri*
† " *alpina*
Pseudocymopterus montanus
Pseudocymopterus sylvaticus
† " *Tidestromii*
Pseudopteryxia anisata
" *longiloba*
Oxypolis Fendleri
†*Angelica Grayi*
Conioselinum scopulorum
" *coloradense*
†*Primula angustifolia*
Androsace pinetorum
†*Anthropogon barbellatum*
†*Amarella monantha*
†*Condrophora Fremontii*
† " *americana*
Dasystephana Parryi
Ploemonium delicatum
" *foliosissimum*
† " *confertum*
" *miletum*
† " *Brandegei*
Gilia globularis
†*Phlox condensata*
Phacelia nervosa
†*Eritrichium argenteum*
Mertensia polyphylla
† " *lateriflora*
† " *Bakeri*
† " *nivalis*
† " *viridula*
† " *Parryi*
† " *alpina*
†*Pentstemon Hallii*
† " *stenosepalus*
† " *Harbourii*
† " *caespitosus*
Chionophila Jamesii
†*Besseya alpina*
" *plantaginea*

Besseya Ritteriana
Castilleja brunnescens
" *confusa*
† " *puberula*
†*Pedicularis Parryi*
" *Grayi*
† " *scopulorum*
Valeriana acutiloba
Campanula Parryi
Coleosanthus umbellatus
Solidago decumbens
†*Tonestus pygmaeus*
Oreochrysum Parryi
Chrysopsis alpicola
" *asprella*
Pyrrocoma Clementis
Townsendia grandiflora
Aster Canbyi
†*Erigeron pinnatisectus*
† " *melanocephalus*
† " *leiomeris*
" *glandulosus*
" *elatior*
" *superbus*
" *formosissimum*
Hymenopappus cinereus
†*Rydbergia Brandegei*
†*Artemisia Pattersonii*
†*Artemisia saxicola*
Arnica macilenta
" *ovata*
Senecio chloranthus
" *pudicus*
† " *amplectens*
" *pagosanus*
† " *Holmii*
† " *taraxacoides*
" *Soldanella*
" *carthamoides*
" *invenustus*
" *admirabilis*
" *lapathifolium*
" *crassulus*
" *perplexans*
" *anacletus*
" *atratus*
" *foliosus*
† " *Harbourii*
" *Nelsonii*
" *crocatus*
" *Jonesii*
† " *petrocallis*
" *pentadontus*
† " *werneriaefolius*
" *ambrosioides*
" *multicapitatus*

5. LOCAL ENDEMIC SPECIES

The following are rare and local species which have been collected at only one or two localities within the Canadian Rockies or the states mentioned below:

Canadian Rockies

†*Wahlbergella attenuata*
†*Cassiope saximontana*
†*Douglasia nivalis*
†*Mertensia Drummondii*
†*Antennaria chlorantha*
" *acuta*

Montana

†*Potentilla Vreelandii*
Dodecatheon uniflorum
Pedicularis Canbyi

Idaho

Allium simillisimum
Romanzoffia Leibergii
†*Tonestus laceratus*

Wyoming

†*Oreobroma minima*
Aconitum ramosum
†*Draba ventrosa*
†*Muscaria micropetala*
Potentilla wyomingensis
" *virgultata*
" *Nelsonii*
†*Pedicularis Hallii*
" *lunata*
†*Trifolium scariosum*
Mertensia viridis
Aquilegia larimiensis
†*Erigeron flabellifolius*
Arnica tenuis

Utah

†*Wahlbergella Kingii*
Aquilegia scopulorum
Delphinium attenuatum
Capnorchis brachycarpum
Lesquerella Wardii
†*Draba sobolifera*
" *brachystylis*
Gormannia debilis
Edwinia macrocalyx
Potentilla paucijuga
†*Synthyris pinnatifida*
Castilleja viscida
" *parvula*

Colorado

Poa callicroa
" *pudica*
" *tricholepis*
Allium Pikeanum
Alsine polygonoides
Radicula curvipes
Radicula Underwoodii
Arabis oblanceolata
†*Potentilla tenerrima*
† " *minutifolia*
†*Trifolium bracteolatum*
†*Trifolium attenuatum*
†*Aragallus Hallii*
†*Polemonium Grayanum*
Besseya reflexa
Chaenactis peduncularia

One of the strangest distributions is that of *Viola biflora*, a European species, which has been collected in America only at a few places in Colorado and in Alaska.

SUMMARY

The subalpine flora contains over eight hundred species. Of these about 30 per cent. are also found above the timberline and

about 60 per cent. are also found in the Montane Zone or pine belt. This leaves only about 10 per cent., which are restricted to the Subalpine Zone. The percentage of characteristic subalpine species is, however, larger, probably 25 per cent. or 30 per cent. of the number, for the 30 per cent. growing above the timberline is divided into two categories, alpine plants descending below the timberline, and subalpine species ascending above the same. So are also some of the plants which are common to the Subalpine and Montane Zones, essentially subalpine, though they descend into the upper part of the Montane Zone. A small proportion is even common to the three zones, and a few, as for instance *Poa crocata*, range from the plains to the alpine regions.

Of the eight hundred species, over 20 per cent. are transcontinental plants, and of these the larger part, about 15 per cent. of the whole number, extend as far south as Colorado and scarcely 2 per cent. are confined to the Canadian Rockies. About one hundred species are common to the old world. Besides the transcontinental element nearly 20 per cent. more are common to some part of the Rocky Mountain region and some part of the Pacific mountains. Of these about 5 per cent. are equally distributed throughout both provinces and 6 per cent. limited to the northern part of both. The remainder is about equally divided between Rocky Mountain plants which have invaded the Cascades and Pacific plants found in the Northern Rockies.

The strictly endemic species constitute nearly 60 per cent., and if those which have invaded the Pacific mountains are added the endemic element comprises about 70 per cent. of the flora. Of the 60 per cent. of strictly endemic plants fully one half are restricted to the Southern Rockies, fully one fourth common to both, and less than one fourth restricted to the Northern.

Of the trees and shrubs found in the Subalpine Zone, eighteen are transcontinental, eighteen are common to the Pacific mountains or emigrants from them, nine are immigrants into the Canadian Rockies from arctic regions, and eighteen are endemics, five of which have invaded the Cascades. Of the endemics, eight are common to both the northern and the southern Rockies, and five are limited to each region; none of them are strictly local.

NEW YORK BOTANICAL GARDEN

Branched prothallia in the Polypodiaceae*

ELIZABETH D. WUIST

(WITH FIFTEEN TEXT FIGURES)

INTRODUCTION

Branching in the early stages of the gametophytes of the Polypodiaceae has received little attention in the literature. Branching in older prothallia by means of adventitious outgrowths arising from any part of the prothallium has been described for various genera by Wiegand ('49), Hofmeister ('51), Kny ('70), Goebel ('77), De Bary ('78), Bauke ('78), Dodel-Port ('80), Klebs ('93), Heim ('96), Lagerburg ('06), Pace ('10), Heilbronn ('10), Fischer ('11), Schlumberger ('11), Wuist ('13), Pickett ('14), and Black ('15). Few cases have been cited where branching took place at an early period in the development of the gametophyte, except in the case of *Vittaria* which has been described and figured by Britton and Taylor ('02). As it is characteristic of the prothallia of that genus to branch extensively, resembling in this respect the gametophytes of the Hymenophyllaceae, no examples will be cited. Among the other genera of the Polypodiaceae the following cases of branching, while the prothallia were still in the filamentous stage, have been noted. Beck ('80) described branched prothallia of *Scolopendrium vulgare* Sm., while Klebs ('93) by means of weak light obtained, in *Polypodium aureum* L., branched prothallia with adventitious outgrowths. Atkinson ('94) observed "in *Adiantum cuneatum* . . . some curious forms of starved prothallia," and added: "In one case, first noted by a student, the protonemal thread forked a short distance from the spore, and the branches extended at right angles to the primary thread like the arms of the letter T, each arm bearing a prothallium. In another case observed the young prothallium produced nearly colourless protonemal threads from marginal cells. Each of these threads bore a prothallium, and in turn produced marginal threads

* Contribution from the Osborn Botanical Laboratory.

bearing other prothallia." Lagerburg ('06) figured a slightly branched filamentous male gametophyte of *Pteridium aquilinum* (L.) Kuhn. Pace ('10) described branched filamentous prothallia of an unknown genus, and Black ('15) observed extensive branching among the filamentous prothallia of *Onoclea sensibilis* L. which had grown in a submerged condition in cultures of distilled water.

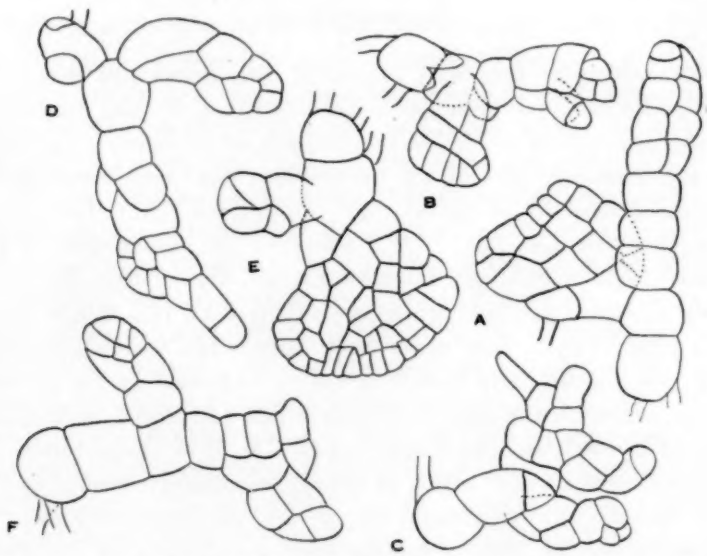

FIG. 1. Branched prothallia of *Onoclea sensibilis* L., × 125.

MATERIAL

The branched prothallia described in this paper occurred in cultures which had been made for the study of the comparative length of the filamentous stage in various genera of the Polypodiaceae. The genera which showed a tendency to branch were the following: *Adiantum*, *Asplenium*, *Camptosorus*, *Onoclea*, *Phegopteris*, *Polypodium*, *Pteridium*, *Scolopendrium*, *Woodsia* and *Woodwardia*. The spores of these various genera were obtained from several sources. Those of *Adiantum* were secured from the greenhouse of the botanical department, Cornell University, and those of *Phegopteris* came from a lawn in Ithaca, New York. The spores of *Camptosorus* and *Scolopendrium* were collected in eastern New York by Mr. Ten Eyck Burr; while those of *Asplenium*, *Onoclea*,

Pteridium and *Woodsia* were obtained from the wild botanical gardens of Minneapolis, Minnesota, through the courtesy of Miss Eloise Butler. The spores of *Woodwardia* were collected near Ann Arbor, Michigan.

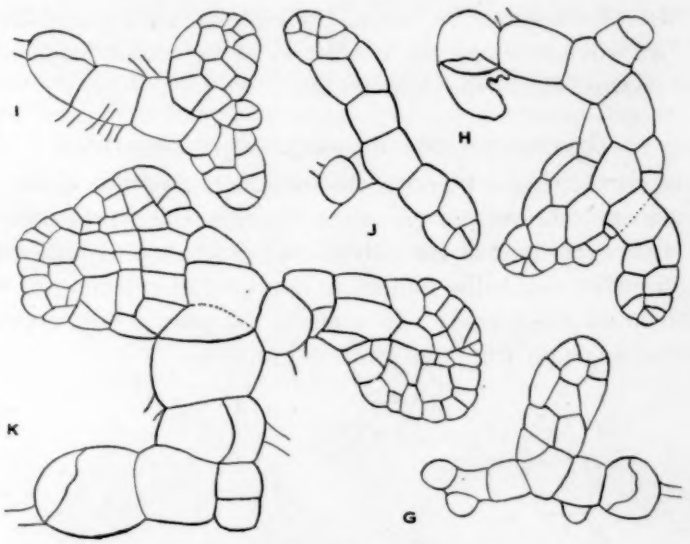

FIG. 2. Branched prothallia of *Onoclea sensibilis* L., × 125.

Cultures of these genera were made by sowing the spores on distilled water and on soil. A series of cultures of *Camptosorus*, *Phegopteris*, *Pteridium*, *Onoclea*, *Scolopendrium*, and *Woodwardia* were made by sowing the spores on Knop's and Prantl's full solutions and on certain modifications of these solutions.

The formulas used in making up Knop's and Prantl's ('81) nutrient solutions are as follows:

Knop's Solution		Prantl's Solution	
$MgSO_4$	0.25 g.	K_2SO_4	0.7 g.
$Ca(NO_3)_2$	1.00 g.	NaCl	0.23 g.
K_2HPO_4	0.25 g.	$CaSO_4$	0.7 g.
KCl	0.12 g.	$MgSO_4$	0.5 g.
$FeCl_3$	trace	Na_3PO_4	0.5 g.
		NH_4NO_3 solution, 0.064 per cent.	20 c.c.

The modifications employed were the following:

Knop's Solution
(*a*) $Ca(NO_3)_2$ omitted

Prantl's Solution
(*a*) NH_4NO_3 omitted
(*b*) NaCl and Na_3PO_4 omitted
(*c*) NaCl omitted
(*d*) Na_3PO_4 omitted
(*e*) $CaSO_4$ omitted

After the spores were sown, the cultures were placed before an east window where the conditions of light and temperature were approximately the same for all.

DESCRIPTION OF THE BRANCHED PROTHALLIA

In all the cases observed, the germination of the spores, the manner and the rate of growth in the branching prothallia did not differ from that of the unbranched prothallia. Neither were the branched prothallia limited to one kind of culture, but were found in all three kinds. In some of the genera they appeared simultaneosluiyn the three kinds of cultures.

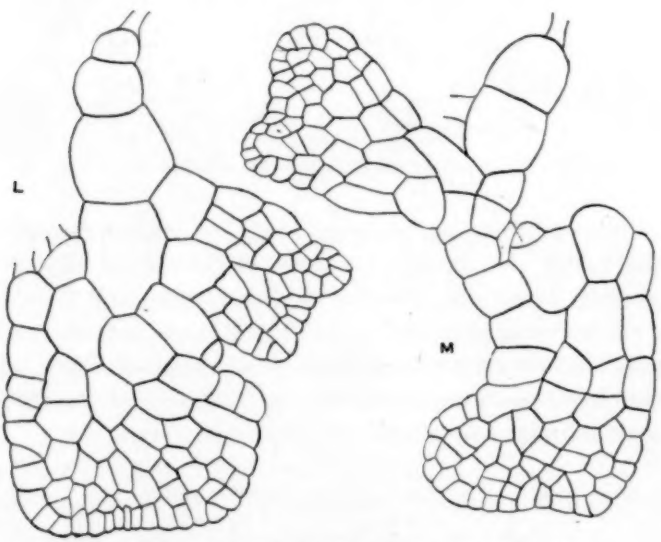

FIG. 3. Branched prothallia of *Onoclea sensibilis* L., × 75.

Onoclea sensibilis L.—The prothallia of this species both on the distilled water and the soil cultures showed a decided tendency to branch. Likewise, the branches showed a great diversity of origin and form, and the beginnings of apical cells or more advanced

apical growth was present in all of them. The branched prothallia shown in FIGS. 1, A–F; 2, G–J; 4, N–Q; and 5, R–T, developed on the distilled water cultures, while those in FIGS. 2, K; 3, L, M; and 5, U, developed close to the inner pot wall on the soil cultures. FIG. 1, A, D, shows branched prothallia whose branches originated in the second cell of the filament. In these prothallia the branches tended to form immediately a plate of cells, while the cells of the filaments continued to divide transversely until three and five cells were formed before they developed an expanded region. In FIG. 1, B, C, while the first branches developed from the second cell of the filament, later branches were given off by the expanded portions of the prothallia. FIG. 1, D, shows not only the development of a branch from the second cell of the filament but also

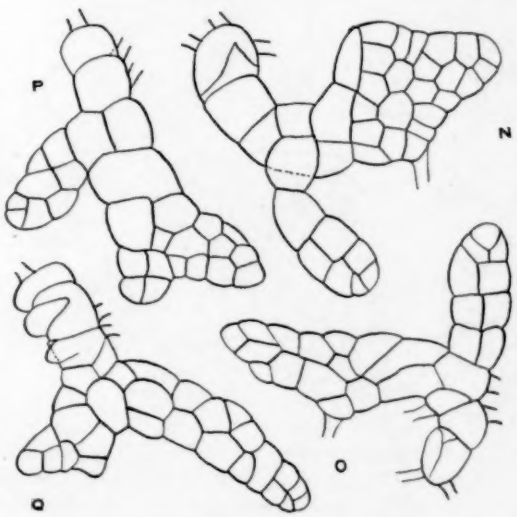

FIG. 4. Branched prothallia of *Onoclea sensibilis* L., × 125.

the tendency of the prothallium to revert to a filamentous stage after a small plate of cells has been formed, if the nutrition is not sufficient to meet its needs. In FIGS. 1, F; and 2, G, H, it seems characteristic for the first branch to originate in the third cell of the filament. However, other branches developed from the more expanded portion of the prothallia. FIG. 2, I, J, shows pronounced cases of dichotomous branching which occurred where

the filament usually gave rise to the expanded portion of the prothallium. In both of these cases the branches originated in the third cell of the filament. In FIG. 2, J, the group of cells at the apex between the branches indicate that there will be a continuation of the main growth of the prothallium. In FIGS. 2, K, and 3, L, M, dichotomous branching developed at a slightly later stage after the first divisions of the expanded portion of the prothallia had been formed. FIG. 4, N–Q, show single lateral branches which appear to have originated at about the same period in the development of the prothallia as the dichotomous branches shown in FIGS. 2, K, and 3, L, M. FIG. 5, R, S, shows branches developed from the expanded portions of the prothallia. In FIG.

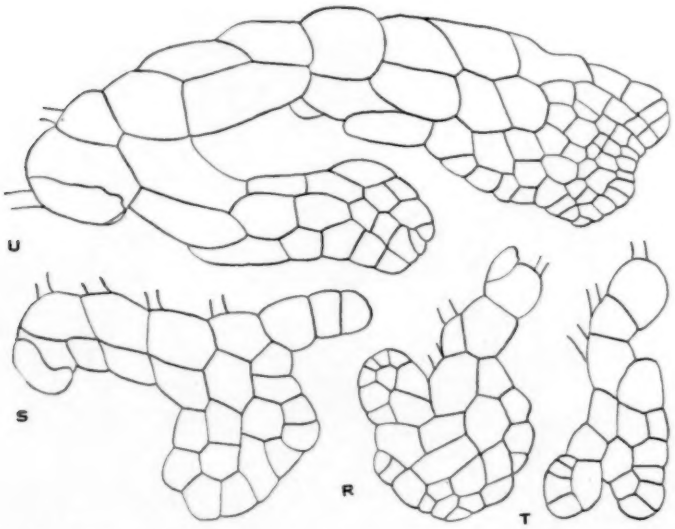

FIG. 5. Branched prothallia of *Onoclea sensibilis* L. R–T, × 125; U, × 75.

5, R, the branch formed a plate of cells while in FIG. 5, S, it tended to assume a filamentous character. FIG. 5, T, shows another case of dichotomous branching but at a later stage in the development of the prothallium. Here it occurred at the apex of the expanded region of the young prothallium. FIG. 5, U, is unique in that the branch appears to have originated in the first, second and third cells of the filament.

Adiantum bellum Moore.—Branched prothallia in the various species of *Adiantum* studied occurred only on the distilled water cultures. In FIG. 6, A, is shown the only case of branching which was observed *in A. bellum*. Here the filamentous branch originated in the first cell of the filament.

Adiantum Capillus-Veneris L.—Examples of branching among the prothallia of this species were frequently observed. In all cases the branching was monopodial and in the majority of cases, as shown in FIG. 6, B–G, the branches developed from the second cell of the filament. FIG. 6, C–E, shows the manner of develop-

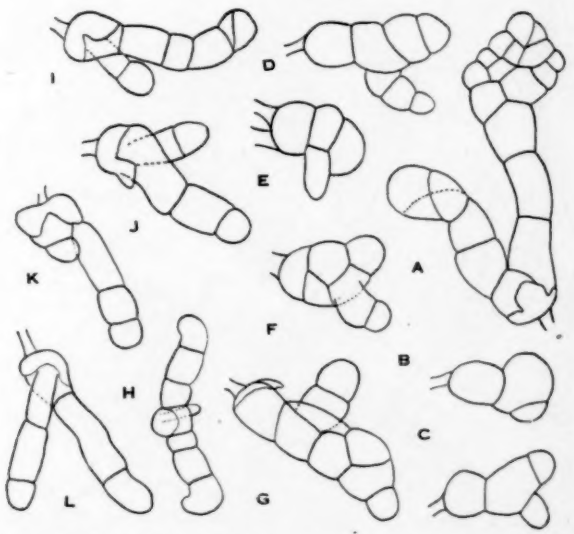

FIG. 6. A. Branched prothallium of *Adiantum bellum* Moore, × 175. B–G. Branched prothallia of *A. Capillus-Veneris* L., × 125. H. Branched prothallium of *A. cardiochloena* Kunze, × 125. I–L. Branched prothallia of *A. cuneatum* Langsd. & Fisch., × 125.

ment of the branch and likewise the continued growth of the main filament. In FIG. 6, F, no filament had been developed; the second cell divided to form the beginnings of the expanded portion of the prothallium. From this expanded region the branch was given off.

Adiantum cardiochloena Kunze.—FIG. 6, H. Here the branch developed from the cell which was cut off by the formation of a vertical wall in the second cell of the filament.

Adiantum cuneatum Langsd. & Fisch.—FIG. 6, I–L. Branching in this species occurred at an early stage in the development of the prothallia. The branches originated in the first cell of the filament and the growth in all cases was very rapid. In FIG. 6, L, is shown a prothallium with a branch as long as the main filament.

Adiantum trapeziforme L.—FIG. 7, A–G, represents branched prothallia of this species. Here branching was both dichotomous and monopodial. In FIG. 7, E, is shown an unusual case of dichotomous branching where both branches tended to grow in the same direction.

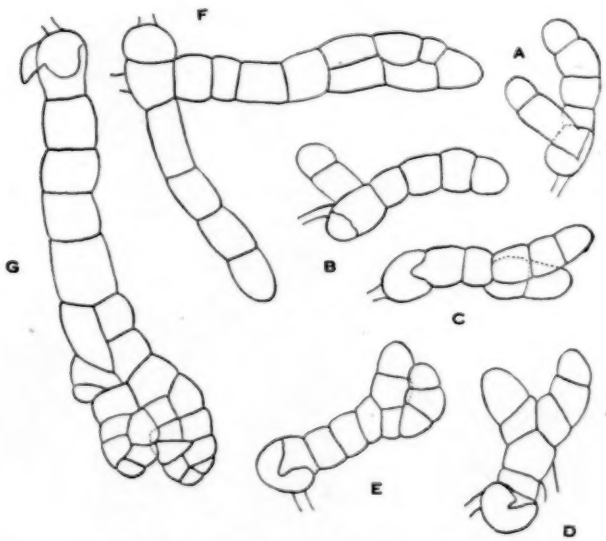

FIG. 7. Branched prothallia of *A. trapeziforme* L., × 125.

Camptosorus rhizophyllus (L.) Link.—FIG. 8, A–D, shows branched prothallia of this species which developed on the distilled water cultures, while FIG. 8, E, shows a prothallium which developed on the inner surface of the pot wall of the soil cultures. FIG. 8, A–D, shows the beginnings of branching in very young prothallia. Branching in two of the cases was dichotomous and in the other two cases monopodial. A few days after the spores were sown on the distilled water, germination took place in the normal manner. In FIG. 8, A, the first prothallial cell instead of dividing by a trans-

verse wall to form a filament of two cells, cut off by two oblique longitudinal walls, a branch cell on either side. FIG. 8, B, C, shows similar cases, however in FIG. 8, B, the second instead of the first prothallial gave rise to the branches. In FIG. 8, C, both the second and third cell each gave rise to a branch while the third cell of the filament continued the growth of the prothallium. In FIG. 8, D, the branch cell which developed from the first prothallial cell divided immediately to form the beginning of a plate of cells. The branched prothallium shown in FIG. 8, E, is in a much more

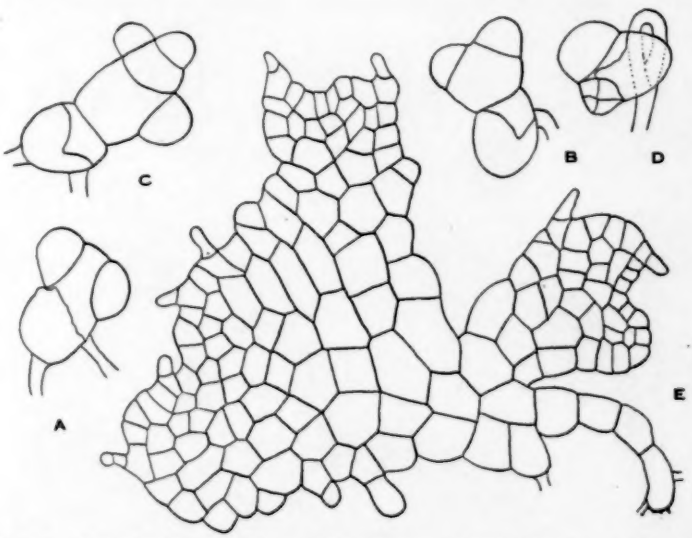

FIG. 8. Branched prothallia of *Camptosorus rhizophyllus* L. A–D, × 125; E, × 75.

advanced stage of development. Here a filament of four cells was formed, then a plate of cells developed. From this plate, early in its development, a lateral branch was cut off which in turn formed an expanded prothallium. The original plate of cells continued its growth into a broad prothallium which showed a decided tendency to branch at its apex.

Asplenium Filix-femina (L.) Bernh.—The branched prothallia of *A. Filix-femina* were observed on both the soil and distilled water cultures. FIG. 9, A, B, developed on the distilled water cultures and FIG. 9, C, on the inner surface of the pot

wall where the light conditions were good and the prothallium was not crowded by other prothallia. FIG. 9, A, shows a young branched prothallium of about twenty cells, which had formed a filament of three cells in the usual manner before the expanded portion of the prothallium developed. The second cell of this filament gave rise to a filamentous branch of three cells; the terminal one of which divided by two oblique longitudinal walls to form the beginnings of an apical cell. From the first cell of the branch was cut off laterally a cell which would later develop into

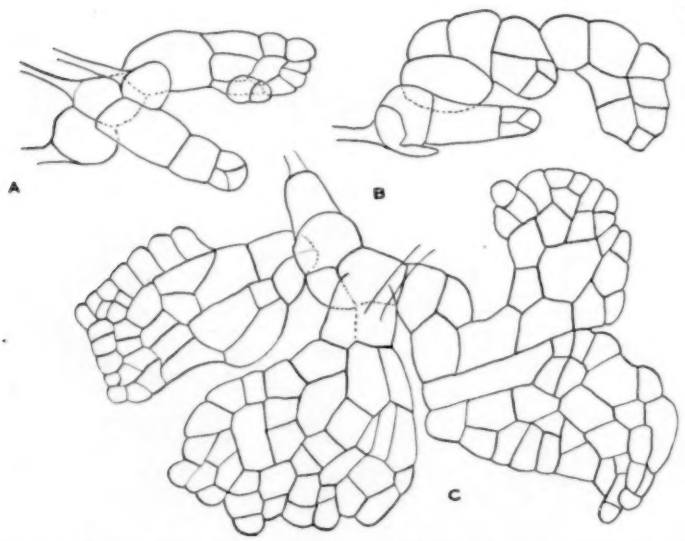

FIG. 9. Branched prothallia of *Asplenium Filix-femina* (L.) Bernh., × 75.

another branch. The expanded portion of the prothallium also gave rise to a short filamentous branch of two cells.

In FIG. 9, B, a short filament of three cells was first formed by transverse divisions, then the third cell divided in such a manner as to form the beginnings of an apical cell. In the meantime a cell was cut off laterally from the first cell of the filament. By transverse and longitudinal divisions this branch developed becoming two cells in width and forming at the apex the beginnings of an apical cell. An extreme case of branching is shown in FIG. 9, C. A filament of three cells formed in the usual manner. From the

second cell there was cut off laterally a cell which developed immediately by longitudinal and transverse divisions into an expanded branch with a definite growing region at the apex. The third cell of the original filament divided by a longitudinal division into two cells, a larger and a smaller one. From the larger of these two cells a branch developed which formed another expanded prothallium whose growing point was not definitely marked. In the meantime the growth of the primary prothallium had continued and an expanded part was formed showing a decided tendency to branch dichotomously at the apex.

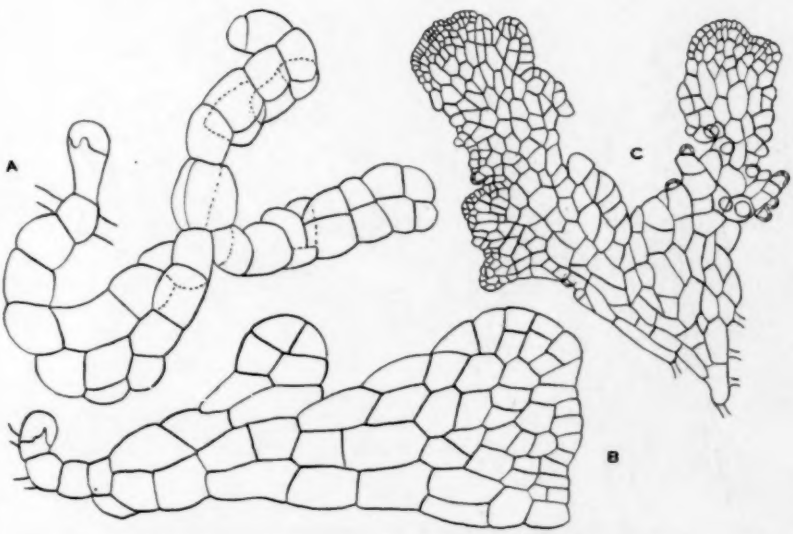

FIG. 10. A, B. Branched prothallia of *Asplenium bulbiferum* Forst., × 75. C. Branched prothallium of *Asplenium platyneuron* (L.) Oakes, × 75.

Asplenium platyneuron (L.) Oakes.—FIG. 10, C, shows a prothallium of this species which developed in a crowded region on a soil culture. In this case branching occurred at a later period in the development of the prothallia. No filament was formed in the early development of the prothallium, but the second cell by division gave rise immediately to the beginnings of an expanded cell plate which during development branched dichotomously. Each branch in turn formed a distinct growing region at its apex.

Asplenium bulbiferum Forst.—The two examples of branched prothallia which are shown in FIG. 10, A, B, developed on the distilled water culture. In both cases the branches originated after the expanded portion of the prothallia had been formed. In FIG. 10, A, the branching was dichotomous. This example is especially interesting as showing the tendency of the prothallium to revert to a filamentous condition at the time of the formation of the filamentous branch. In FIG. 10, B, branching was monopodial and the branch tended to form immediately a plate of cells.

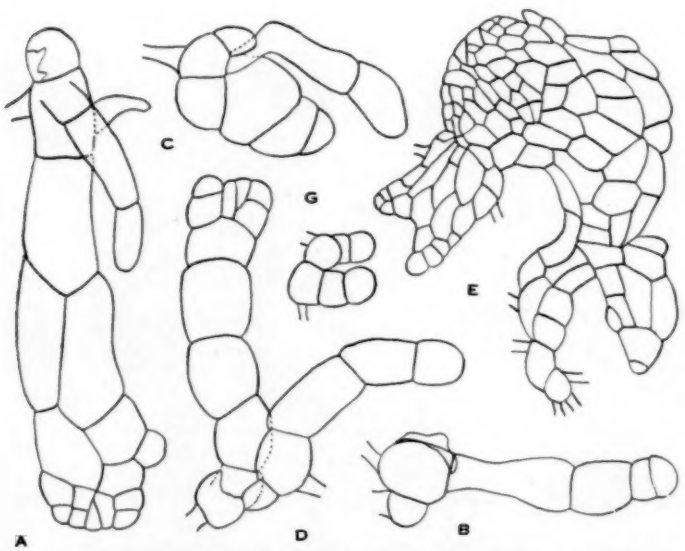

FIG. 11. A–E. Branched prothallia of *Phegopteris polypodioides* Fée, × 125. G. Branched prothallium of *Polypodium aureum* L., × 125.

Phegopteris polypodioides Fée.—The branched prothallium which is shown in FIG. 11, A, occurred in an uncrowded region of the soil culture while those shown in FIGS. 11, B–E, and 12, F, developed in modified Prantl's solutions. FIG. 11, B–D, was found in the Prantl's solution with K_2SO_4 omitted, while FIGS. 11, E, and 12, E, occurred in Prantl's solution from which $CaSO_4$ had been omitted. In all cases observed the branching was monopodial. In FIG. 11, A, the branch was filamentous in form and originated in the second cell of the filament. FIG. 11, B, shows

the origin of the branch from the first cell of the filament and FIG. 11, D, shows the further development of this branch into a filament of five cells. In FIG. 11, C, is shown an interesting example of branching. Here the first prothallial cell instead of dividing by a transverse wall into two cells, divided by means of a longitudinal wall, thus forming two cells side by side. One of these cells by growth and transverse division continued the growth of the filament while the other gave rise to two branches. One formed a filament of two cells, the first of which was extremely long. In FIGS. 11, E, and 12, the branches were not formed until

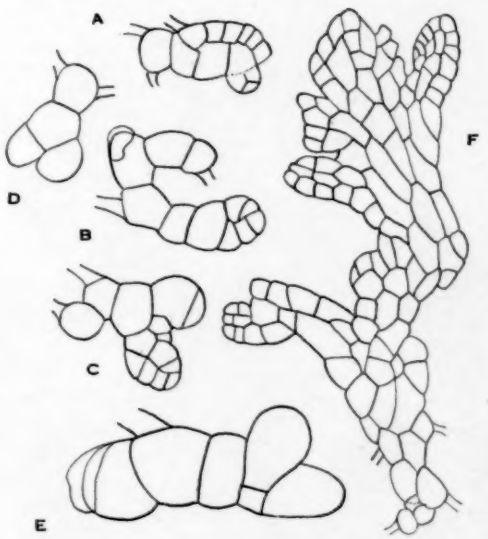

FIG. 12. A–E. Branched prothallia of *Woodsia obtusa* (Spreng.) Torr., × 125. F. Branched prothallium of *Phegopteris polypodioides* Fée, × 75.

the expanded portion of the prothallia had begun to develop. In FIG. 12, the expanded portion later showed a decided tendency to branch monopodially at its apex.

Polypodium aureum L.—Only one case of branching was observed in this species and it developed on the distilled water culture. As shown in FIG. 11, G, the branch originated in the first prothallial cell. The rate of growth was the same for both the main filament and the branch.

Woodsia obtusa (Spreng.) Torr.—All the cases of branched prothallia of *Woodsia obtusa* were observed on distilled water cultures; in two cases branching was dichotomous while in the other three cases it was monopodial. FIG. 12, B, shows the branch originated from the first cell of the filament. In FIG. 12, A, the branch originated from the slightly developed cell plate. FIG. 12, C, D, shows different stages in the development of the dichotomous branches. FIG. 12, E, was an interesting case of branching. Here the wall which cuts off the branch from the main filament did not form at the usual place, but formed almost in the center of the filament cell which gave rise to the branch.

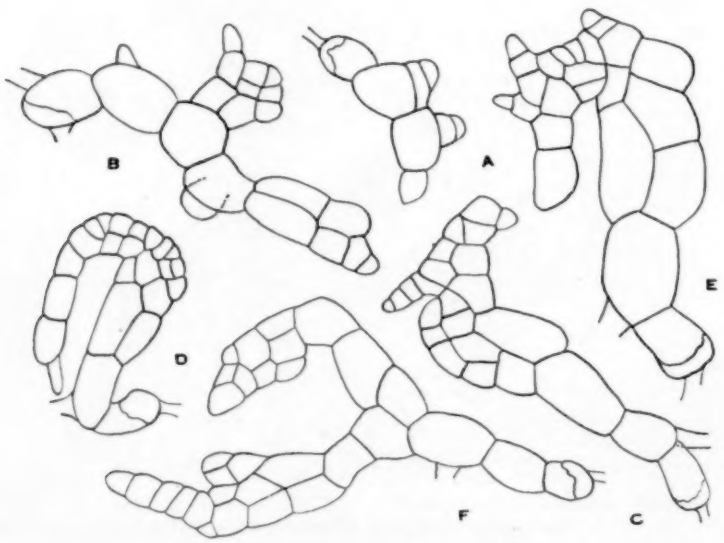

FIG. 13. Branched prothallia of *Scolopendrium vulgare* Sm., × 125.

Scolopendrium vulgare Sm.—All cases of branching in this genus were observed on Prantl's solution with $CaSO_4$ omitted. FIG. 13, A–E, shows typical examples of the types of branching found in these cultures. FIG. 13, A, is interesting as showing the tendency of both the second and third cells of the filament to form monopodial branches with very short cells. In FIG. 13, B, the branch which originated from the third cell of the filament formed immediately a plate of cells which in turn showed a tendency to

branch at one side of the apex. FIG. 13, C, shows the origin of a branch from the apex of the expanded portion of the prothallium, while FIG. 13, D, E, shows further development of such a branch. These branches formed a small plate of cells, two rows in width, then tended to revert to a filamentous condition, at the same time growing downward, thus giving the appearance of two young prothallia attached by their apexes. FIG. 13, F, shows the only case of dichotomous branching which was observed. One of the branches reverted from a plate of cells to a filament four cells in length.

Woodwardia virginica (L.) Sm.—The branched prothallia of

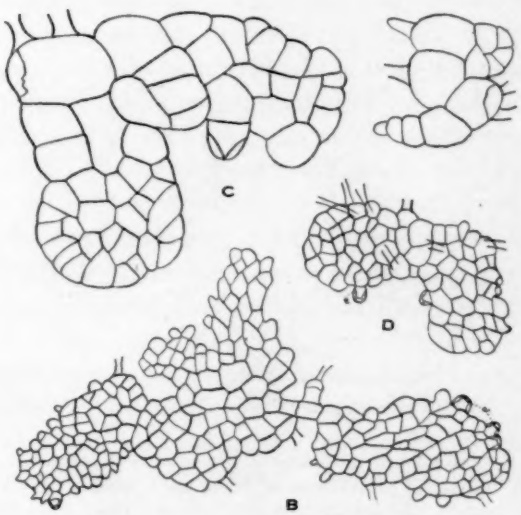

FIG. 14. Branched prothallia of *Woodwardia virginica* (L.) Sm. A, D, × 125; B, C, × 75.

Woodwardia virginica varied in size and shape and showed a decided tendency to branch dichotomously. Those shown in FIG. 14, A–D, and 15, E, F, developed on the inner surface of the pot wall of the soil culture. They were not crowded by other prothallia and were well lighted. FIG. 15, G, developed on Prantl's nutrient solution with $CaSO_4$ omitted. In FIG. 14, A, B, branching took place from the first and second cells of the filament. In FIG. 14, C, D, and 15, G, branching took place after the plate of

cells had begun to develop, while in FIG. 15, E, F, branching occurred much later in the development of the prothallia.

Pteridium aquilinum (L.) Kuhn.—The only example of branching observed in this species was on Prantl's full solution (FIG. 15, H). Here the branch developed from the second cell of the filament and seemed to show a more vigorous growth than the main filament. The branch formed a short filament of two cells, then developed the beginnings of an expanded region while the

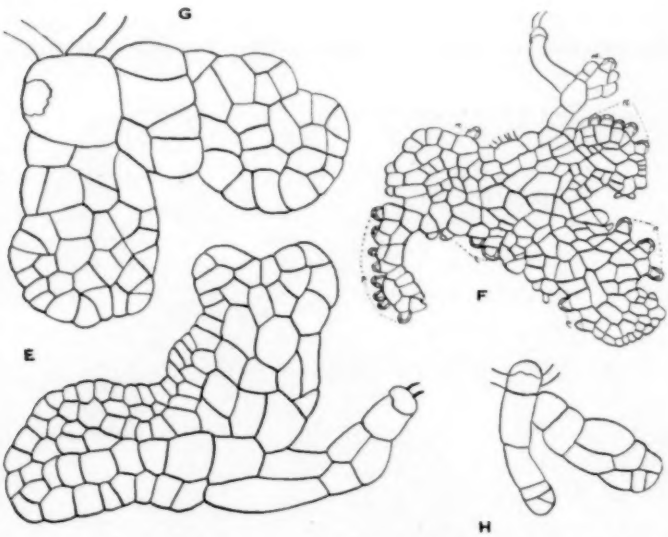

FIG. 15. E–G. Branched prothallia of *Woodwardia virginica* (L.) Sm., × 75; *a*, antheridia. H. Branched prothallium of *Pteridium aquilinum* (L.) Kuhn, × 125.

main filament developed three cells of irregular length before cutting off the beginnings of an apical cell. This slowness in growth and the irregularity of length of the cells of the filament would seem to indicate a poorly nourished condition of the main filament.

DISCUSSION

A comparison of the previously described branched prothallia with those found by other writers would seem to indicate that whatever factor, or set of factors, working separately or together, may have been the determining ones, the development of branches

was associated with conditions of the environment. In Klebs's experiment weak light seemed to have been the cause of branching. Light may be the determining factor in branching where the prothallia are crowded and therefore shaded by other prothallia, but it can not be considered the determining factor in all the cases described in this paper, for the majority of these branched prothallia occurred in uncrowded regions of the cultures under good light conditions. However, all the branched prothallia except one developed on cultures of distilled water or nutrient solutions, from which some chemical element had been omitted; while all but two of the branched prothallia on the soil cultures were found on the inner surface of the pot wall. This is especially interesting as indicating that other factors than light entered into the problem. Atkinson designates the branched prothallia of *Adiantum* as "starved prothallia," which would seem to indicate that they had developed under poor nutritive conditions. Miss Black suggested the possibility of a lack of oxygen as the determining factor in the production of the branched prothallia in her cultures. This explanation would not hold good for the present cases, as all three cultures, distilled water, soil, and nutrient solution, were covered with loosely fitting glass plates and, since the prothallia were not submerged in the nutrient solution or distilled water they received a sufficient supply of oxygen.

As branching was not observed in the nutrient solution cultures, where all the chemical elements necessary for growth were present in sufficient quantities to meet the needs of the prothallia; as few cases of branching were observed among the prothallia of the soil cultures, in positions which appeared favorable for nutrition, it would seem as if there was an intimate connection between nutrition and branching, that poor nutritive conditions accelerated the stimulus of branching, and that good nutritive conditions weakened the stimulus. However, it is impossible to say just what factor of nutrition was the determining one; for even by cultivating prothallia on nutrient solutions whose chemical formula are known, we do not know the physiological effect from the chemical reactions due to the presence or absence of various chemical elements.

SUMMARY

1. Branched prothallia occurred in cultures of *Adiantum bellum*, *A. Capillus-Veneris*, *A. cardiochlaena*, *A. cuneatum*, *A. trapeziforme*, *Asplenium bulbiferum*, *A. Filix-femina*, *A. platyneuron*, *Camptosorus rhizophyllis*, *Onoclea sensibilis*, *Phegopteris polypodioides*, *Pteridium aquilinum*, *Scolopendrium vulgare*, *Woodsia obtusa*, and *Woodwardia virginica*.

2. Branched prothallia were not confined to one type of culture medium, but developed on distilled water, on soil and on nutrient solutions.

3. Branches were not developed at any definite period in the life history of the prothallia, but were formed: (*a*) by any cell of the filament; (*b*) by divisions of the last cell of the filament; (*c*) from the margin and apex of the expanded portion of the prothallium.

4. Branching was both dichotomous and monopodial.

5. A definite relation seemed to exist between branching and nutrition.

In conclusion I wish to express my thanks to Professor Alexander W. Evans of Yale University and to Dr. C. H. Kauffman of the University of Michigan, to both of whom I am indebted for valuable suggestions in the preparation of this paper.

YALE UNIVERSITY

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A new species of Pritchardia

JOSEPH F. ROCK

(WITH PLATE 21 AND ONE TEXT FIGURE)

The genus of palms, *Pritchardia*, is represented in the Hawaiian Islands by eleven species, including the new species treated in this paper. Originally, there were only two species known from these islands, *Pritchardia Gaudichaudii* Wendl. and *Pritchardia Martii* Wendl.

For several years I have carried on, on all the islands of this group, thorough botanical explorations; these have brought to light several new species of *Pritchardia*, most of which have been described by O. Beccari. Kauai has furnished two species; *P. minor* and *P. eriophora;* Maui, one species, *P. arecina;* Oahu, one species, *P. Rockiana;* and Hawaii, two species, *P. eriostachya* and *P. Beccariana*, the last (which is the handsomest of all) being here described for the first time. Beccari had described previously *P. Hillebrandii* from Molokai, *P. lanigera* from the Kohala Mountains, on Hawaii, and *P. remota* from Bird Island (Moku Manu), northwest of Kauai.

During a sojourn at the Volcano of Kilauea with my friend, M. L. Copeland, whom I take this opportunity to thank for his kind assistance, we discovered this handsome species in the humid forests of Glenwood. I was at once struck by the extraordinary size of this palm, its peculiar inflorescence and large globose fruits. We felled one tree and thus obtained complete specimens, some of which I forwarded to my friend, Dr. O. Beccari, with whom I had had long and interesting discussions of our Hawaiian palms while in Florence less than two years ago. He pronounced the palm a very distinct species but asked me, as he was occupied with other work, to describe it. With his consent I have taken the liberty of naming this beautiful species in his honor.

I believe that the Hawaiian Islands still harbor other species of *Pritchardia*, especially Lanai and the Island of Oahu; future

explorations will doubtless increase our knowledge of this beautiful genus of palms.

Pritchardia Beccariana Rock, sp. nov.

Trunk 20–25 m. tall, about 40 cm. in diameter at the base, cylindrical, grayish, smooth, about 30 cm. in diameter breast-high, with more or less distant rings, showing the attachment of the leaves, the crown of leaves forming perfect globose heads of large dimensions; leaves large, suborbicular, measuring 1.5 m. or more from the ligule to the apex of the median segment, the ligule rotundate and prolonged in the middle to a distinct point; petioles 3 m. long in young fronds, 1.5–2 m. in mature fronds, stout, and covered on the under side with a fawn-colored squamaceous tomentum; segments about sixty, each segment 4–4.5 cm. wide, and subdivided again for 30 cm. into linear-acuminate lobes, with filaments 15–25 cm. long in the bifurcations, the lower surface of the leaves, especially near the petiole and costae covered with a squamaceous, flaky tomentum, upper surface glabrous; spadix 2–3 m. long including a main peduncle of 1 m., the spadix branching into three to five large open panicles at intervals of 3–4 dm.; the terete peduncle 2 cm. in diameter, enclosed by various, tubulose spathes 70–80 cm. long; panicles compressed, loose, the first two or three open and loosely branched, the last two nearest the leaf-axil short and densely branched, the branchlets short and spirally twisted; the former bearing abortive flowers only, the latter, or often only the last panicle producing fertile flowers and mature fruits; each panicle enclosed in several, reddish brown spathes, 30–40 cm., long covered with a squamaceous tomentum on the outside; flowers subsessile, on the more or less tortuous branchlets of the compound panicle, those bearing fertile flowers spirally twisted; calyx 5 mm. long, tubular-cylindrical, truncate at base and apex, with three very short teeth; petals (?); staminal cup much longer than the calyx, exserted 3 mm., and terminating into six, somewhat compressed, filaments, 2 mm. long; anthers acute at the apex, obtuse and slightly notched at the base, 3.5 mm. long, attached at about the middle to the filament; style columnar, triquetrous, with three punctiform stigmas at the apex; mature fruits large, subglobose; black, shining, 4 cm. in diameter, slightly flattened on one side, with a short conical apex; epicarp black, thin, fragile at the maturity of the fruit and exposing the thick, fibrous mesocarp, 5–6 mm. thick at the base, thinner at the apex; endocarp ligneous, 1 mm. thick; cavity of the endocarp circular, slightly flattened at the base, 2.75 cm. in diameter, not situated exactly in the middle of the fruit, but a little nearer to the apex;

seed globose, base slightly broader, dark, brownish black, albumen horny, snow-white, hilum orbicular, embryo situated immediately above the hilum. [PLATE 21 and TEXT FIG. 1.]

ISLAND OF HAWAII: in the rain forests in the neighborhood of Glenwood at an elevation of 3,200 feet; collected flowering and fruiting, December 23, 1914. The type specimen is preserved in the herbarium of the College of Hawaii.

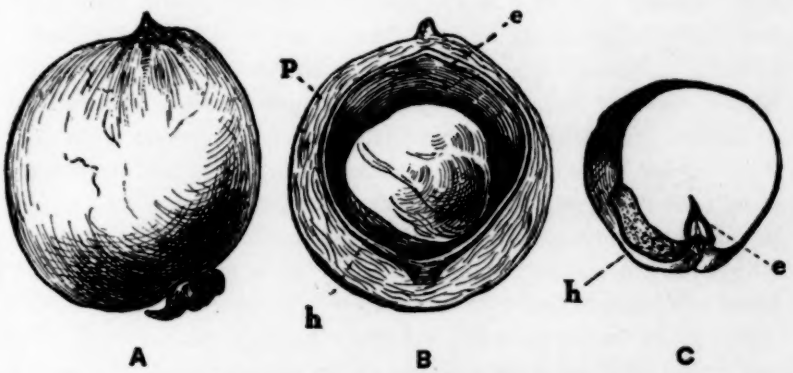

FIG. 1. PRITCHARDIA BECCARIANA Rock

A. Mature fruit, slightly reduced. B. Mature fruit cut in half, showing whole seed, slightly reduced: *p*, pericarp; *e*, endocarp; *h*, hilum. C. Seed cut in half, slightly reduced: *h*, hilum; *e*, embryo.

This exceedingly distinct species is one of the handsomest and tallest of the genus *Pritchardia*. It forms large groves throughout the forest in the vicinity of Glenwood, several hundred feet below the volcano of Kilauea, growing in company with *Metrosideros polymorpha*, *Cibotium Chamissoi*, *Cibotium Menziesii*, etc., towering as high as the tallest *Metrosideros* (Ohia Lehua) trees.

This species differs from all other species of *Pritchardia* mainly in the enormous inflorescence, which branches into five distinct spadices; in the large globose fruits; and in the large dimensions of the plant in general.

COLLEGE OF HAWAII,
HONOLULU, HAWAIIAN ISLANDS

Description of plate 21

Stand of *Pritchardia Beccariana* Rock, growing in the humid forest near Glenwood, Olaa, Hawaii, at an elevation of 3,200 feet. Ferns in the foreground, *Cibotium Chamissoi* and *C. Menziesii;* trees in the background, *Metrosideros polymorpha*.

Botanical work of Dr. E W. Hilgard

ROLAND M. HARPER

Dr. Eugene Woldemar Hilgard, who was born in Zweibrücken, Bavaria, January 5, 1833, and died in Berkeley, California, three days after his eighty-third birthday, was a shining example of a versatile type of scientist, common in the nineteenth century but becoming scarce in these days of increasing specialization. He was best known as a soil investigator and agronomist, but also ranked high as a geologist and chemist, and was pretty well versed in systematic and geographical botany. He was one of the pioneers in the correlation of soils with vegetation in America, and always emphasized the importance of native vegetation as an indicator of the productivity of soils. The fact that the scientific study of soils is almost inseparable from that of plant ecology was more fully appreciated by him than by most American soil investigators now living (some of whom seem to have little or no botanical training, if one may judge by their writings).

His first contribution to botanical science was his 415-page report on the geology and agriculture of Mississippi, published in 1860. In that the soils and vegetation of the several geographical divisions of the state (except the alluvium of the Mississippi River) were described in considerable detail, and it was at the time and for years afterward the best account of Mississippi vegetation in existence. As it was written before the publication of Chapman's Flora of the Southern United States, when there were no very satisfactory manuals for that part of the country (the best available being Darby's), some of the plants were wrongly identified, but a reader familiar with the southern flora can easily make the necessary corrections for himself.

A somewhat similar treatment was employed in a 44-page pamphlet on a geological reconnaissance of Louisiana, published in New Orleans in 1869, and in his descriptions of Mississippi, Louisiana and California, in the fifth and sixth volumes of the Tenth Census (1884), which have never received the attention from botanists that they deserve.

In Garden and Forest for March 7 and June 13, 1888, he had short papers on California forest trees; and a longer account of the weeds of that state by him appeared in the California Experiment Station Report for 1890 (pp. 238–252) and, almost simultaneously, in several numbers of Garden and Forest during the second half of 1891. His paper on the *cienagas* of southern California, published in the Bulletin of the Geological Society of America in 1892 and in the California Experiment Station Report for 1892–1894, is of some botanical interest, as are several papers on deserts and alkali lands in various publications. His review of Fernald's "Soil preferences of alpine plants," in Science for January 24, 1908, shows an intimate knowledge of ecological principles.

His text-book on Soils, with 620 pages and numerous illustrations, published in 1906, is practically a summary of all his researches, and contains much that is of interest and value to botanists.* He contributed many papers on cultivated plants to the reports and bulletins of the California Experiment Station (of which he was director from 1888 to 1904), which it is hardly worth while to enumerate separately.

In the line of botanical discoveries, he is credited by Chapman (Fl. So. U. S. ed. 2, 658. 1883) with being the first to find *Eriocaulon septangulare* in the South.† During his geographical explorations for the "Northern Transcontinental Survey" in Montana and Washington in 1882 he collected a few plants, at least one of which turned out to be undescribed; this was named *Oenothera Hilgardi* by Greene (Bull. Torrey Club **10**: 41. 1883) and afterwards transferred to *Sphaerostigma* by Small (see Piper, Contr. U. S. Nat. Herb. **11**: 18, 406. 1906).

The writer, after corresponding with Dr. Hilgard for several

* See review in Torreya **7**: 170–175. Aug. 1907; and comments in Bull. Torrey Club **40**: 377 *et seq.* Aug. 1913.

† The plant so determined, if collected on his trip to southeastern Mississippi in the spring or early summer of 1859, as seems most likely, may have been another species, perhaps *E. lineare* Small, which was not distinguished until 1903 (see Bull. Torrey Club **32**: 461–463; **33**: 527). For *E. septangulare* grows mostly on sandy shores of lakes and ponds, and blooms in late summer, while *E. lineare* is a typical pine-barren plant, and blooms in April and May. The only southern stations for *E. septangulare* known to the writer are in Lowndes County, Georgia, and Leon, Walton and Santa Rosa Counties, Florida. In Small's Flora it is said to range west to Texas, but this statement lacks verification.

years, had the pleasure of meeting him at his home in Berkeley at the time of the A. A. A. S. meetings last summer, and found him somewhat enfeebled by age but wide-awake mentally. He always wrote for publication in plain simple language, as free as possible from technicalities, and was very modest, sincere and unaffected, as befits a great scientist.

Accounts of his life and work by two of his California colleagues were published in Science for March 31, 1916, and reprinted with some additions, two portraits, and a bibliography of over 250 titles, in the University of California Chronicle, vol. 18, no. 2 (this also issued in June as a separately paged pamphlet with 50 pages). Other recent biographical sketches are in the Experiment Station Record (Washington) for March, 1916, and the Geographical Review (New York) for May. The last contains references to a few earlier ones.

COLLEGE POINT, NEW YORK

INDEX TO AMERICAN BOTANICAL LITERATURE

1915-1916

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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